Early Larval Development of *Polydora nuchalis* Woodwick, a Spionid Polychaete

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THE MOST RECENT detailed work treating the larval development of *Polydora*, that of Hannerz (1956), appeared a little more than one century after Oersted (1843) described for the first time a larval stage in *Polydora ciliata* (Johnston), Wilson 1928. Related papers presented during the interval included those of Claparède (1863), Agassiz (1867), Jacobi (1883), Whitelegge (1890), Andrews (1891), Mesnil (1896), Leschke (1903), Söderström (1920), Wilson (1928), Rioja (1939 and 1941), Hartman (1941), Thorson (1946 and 1950), Smidt (1952), and Casanova (1952). Each of these added information valuable to the understanding of polydorid development, but, as yet, in only a few forms is the early development known in detail.

The purpose of this paper is to make known the early developmental stages of a recently described polydorid, *Polydora nuchalis* Woodwick (1953).

METHOD

The developmental stages of *P. nuchalis* were cultured either in petri dishes containing sea water and sand from the original collecting area or in aquaria of circulating aerated sea water after the method of Reish (1953). Favorable results were obtained with both of these methods.

Observations were made of encased larvae (in egg capsules) as well as free-swimming individuals. The study of living material on depression slides provided specimens unaltered by fixation or cover glass pressure. Drawings of living forms were made employing the technique of Wilson (1928) and were inked following a comparative study of several other larvae of the same age group.

The drawings do not constitute a continuous developmental series from one individual but are a synthesis of a series of observations of individuals from a number of egg cases. The ages assigned the various stages are not absolute but, because they are based on multiple observations, are considered to be reasonable.

COMPOSITE POLYDORA LIFE HISTORY

An understanding of the larval development of polydorids is expedited by an understanding of the relationship of these larval stages to the remainder of the life history. A composite life history of members of the genus is presented below; *P. nuchalis* follows this scheme in most stages but does show individual differences.

A composite life history as extracted from the literature may be summarized in the following manner. An adult male and female copulate. Fertilization is internal. The female spawns the fertilized eggs through the nephridial canal and into transparent capsules. The capsules, formed in the manner described by Söderström (1920), are attached to the inner wall of the female's tube or burrow. Cleavage of the fertilized egg is complete but unequal. Further development of larvae within the egg capsule follows one of two types: (1) In *Polydora ciliata* (Wilson, 1928) and certain other species each egg in the capsule gives rise to a larva. The larvae leave the capsule at the 3-segment (setigerous segment) stage as planktotrophic forms to begin a long planktonic period (four to six weeks) prior to settling and metamorphosis. (2) In *Polydora hoplura* (Wilson, 1928) which represents the other type, each egg in the capsule does not give rise to a larva. The few which do develop, feed on the undeveloped eggs (nurse eggs). The larvae begin feeding at about the 3-segment stage but do not leave the capsule until about the 12-segment stage. The hatched larvae pass through a very short planktonic stage, if any, before settling and metamorphosis.

The latter type of development is found in

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P. nuchalis. Larvae leave the egg capsules after having fed on nurse eggs until the 9- to 12-segment stage (Plate I, Fig. 1). Further studies, to be reported in another paper, suggest that male and female do not copulate as such; a reciprocal transfer of sperm involving two protandric males occurs. The stored sperm fertilize the eggs which develop in the later female stage of protandry in each individual. Protandry and also neoteny have been reported for *Polydora hermaphroditica* Hannerz (1956).

Polydora nuchalis does, however, follow rather closely the composite life history in the remaining development. The larval stages described below are not unlike those figured for other species of *Polydora.*

EARLY DEVELOPMENTAL STAGES OF *Polydora nuchalis*

Egg. (Plate I, Fig. 2.) The eggs are round and about 120 μ in diameter. They include a central mass of light pink yolk granules and a very narrow peripheral region which is transparent. The yolk granules described here appear in the gut of all the developing stages up to at least 10 segments and are useful in determining the developmental boundaries of the gut in all these stages.

Cleavage of the egg is total but unequal as has been reported for other polydorids.

Early Larva, 18 Hours. (Plate I, Fig. 3.) The larva, 180 μ long, is transparent anteriorly, the yolk granules being concentrated in the posterior half. The primordia of the peristomium and prostomium are set off by ridges. This stage has an unusual anteroventral prolongation of the larval body. The prolongation was noted in more than one series of larvae but no suggestion can be made here as to its significance. It may be abnormal, but its repeated appearance and the fact that larvae of this kind continued to develop in a normal fashion later have led to its inclusion to allow comparison with possible future investigations on this and other species. The prototroch is located on the ventrolateral surface near the junction of the main body of the larva and the anteroventral prolongation. The telotroch has appeared also but is lacking from a wide dorsal portion.

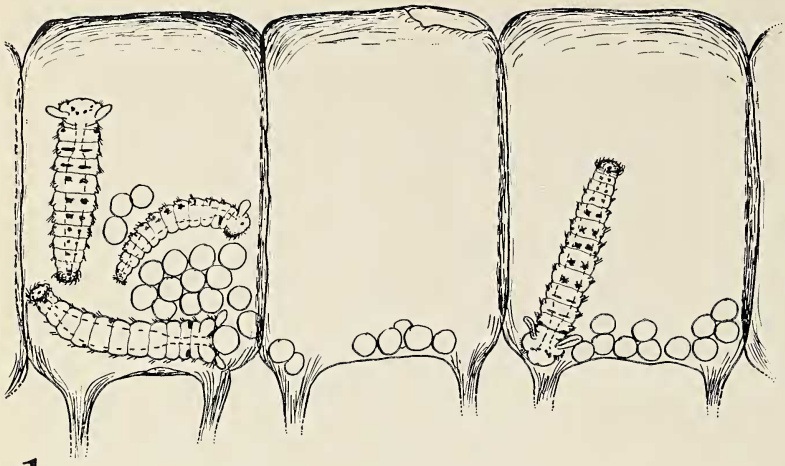
Early Larva, 36 Hours. (Plate I, Fig. 4.) The anteroventral prolongation is no longer present in this stage and the larva measures only 120 μ in length. The anterior part of the larva remains transparent; the posterior part is filled with yolk granules. The prototroch, not apparent in this figure, is limited mainly to the ventral region. The formation of the vestibule and the anterior portion of the gut has been initiated.

Late Presegment Larva, 72 Hours. (Plate I, Fig. 5.) The larva has elongated and does not so closely resemble the egg as did the two preceding larval stages. The larva is about 200 μ long, nearly double the length of the preceding stage; however, it has no true segments as yet. The anterior and the posterior body regions are transparent with the yolk present in the central region serving as an excellent indicator of the intestinal portion of the digestive tract. The transparency of the posterior region is a result of the development of the pygidium. The telotroch is well developed and prominent. The prototroch is present laterally, just posterior to the two eyes. The lateral eyes are the first pigment areas to be formed. Differentiation of the head and body has begun.

Early Two-Segment Larva, Five Days. This larva, 0.26 mm. long, has two complete segments and the beginning of a third pair of setal sacs. Two pairs of eyes are now present in the transparent anterior region. The palpi are beginning to bud laterally just posterior to the eyes. The development of the vestibule has continued; the mouth proper is visible. The posterior gut has begun to invaginate but has not joined the central concentration of yolk granules. The pygidium is set off from the rest of the body by a depression in the body surface which contains the base of the cilia of the telotroch. The first pair of dorsal melanophores is located on the primordia of the third segment.

Three-Segment Larva, Six Days. (Plate II, Fig. 1.) The larva, 0.30 mm. long, has three well-developed segments. It is transparent except for segments two and three in which the gut contains yolk granules.

The palpi have thickened but have not elongated. The protroch and telotroch are as described for the previous stage. The pygidium is cone-shaped and papillated; its appearance is



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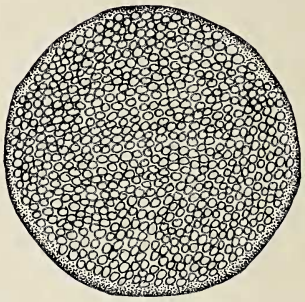

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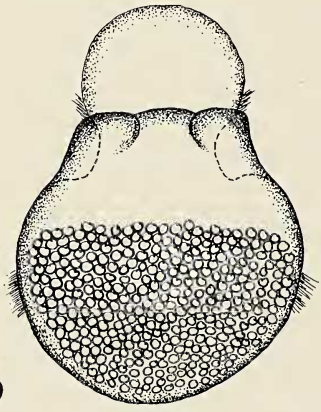

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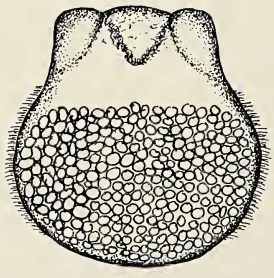

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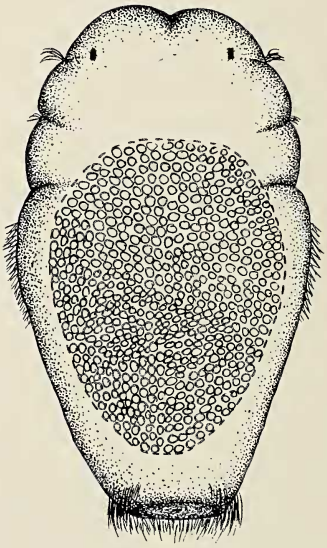

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PLATE I. Fig. 1. Egg capsules and larvae. Fig. 2. Egg, 0.12 mm. Fig. 3. Early larva (18 hours), 0.18 mm. Fig. 4. Early larva (36 hours), 0.12 mm. Fig. 5. Late pre-setiger larva (72 hours), 0.20 mm.

similar to that described by Hartman (1941) for an unknown spionid larva. The melanophores on the third segment have elongated laterally and another pair has formed on the developing fourth segment.

This 3-segment stage has three pairs of eyes. Later, the two pairs which are anterolateral fuse on each side producing a single anterolateral pair. Four eyes, the fused pair and the median pair, are retained throughout life.

The vestibule has enlarged but has not as yet opened to the granular intestinal portion of the gut. The ciliated posterior invagination of the gut nearly reaches the third segment and after a few additional hours of development its cavity becomes joined to that of the granular intestinal portion. This junction, along with completion of the vestibular portion, will produce a functional digestive tract. In larvae having a long pelagic life, completion of the gut development and hatching are concurrent and larvae are able to feed upon leaving the egg cases; this is usually at the 3-segment stage. *Polydora nuchalis* does not hatch at the 3-segment stage but does begin to feed on the nurse eggs. The stage at which gut development is completed, however, is not so critical in a species of *Polydora* having nurse eggs.

Five-Segment Larva, One Week. This larva is about 0.50 mm. in length. It has five setigerous segments and at least three more segments which are forming. The entire animal is transparent except for a few yolk granules present in the gut. Most larvae of this size have a complete digestive tract including a vestibule, esophagus, intestine, rectum, and anus. The vestibule, esophagus, and rectum are greatly ciliated.

The palpi have elongated but the prototroch, telotroch, and pygidium are as described for the preceding stage. Two pairs of eyes are present in the normal adult position with the lateral pair anterior to the median pair.

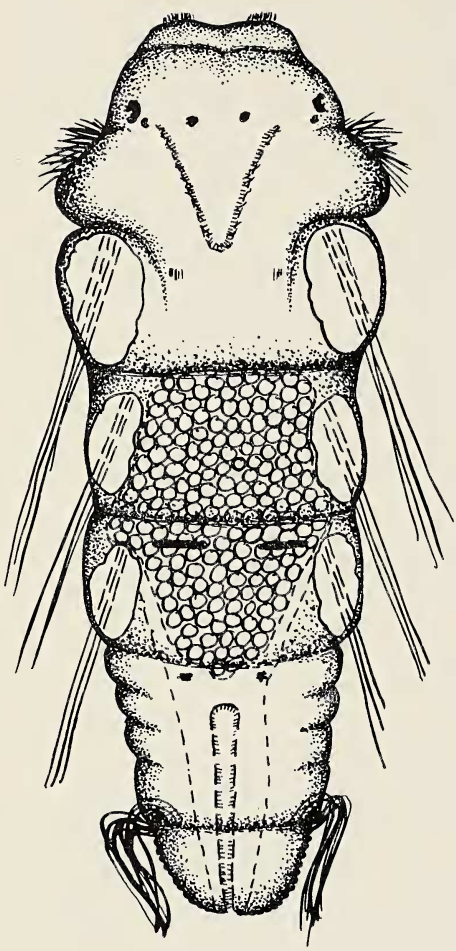
The dorsal paired melanophores are elongated on segment three and smaller pairs are present on segments four and five. There is also a single pygidial melanophore.

Ten-Segment Larva, About Two Weeks. (Plate II, Fig. 2.) This larva is 0.65 mm. in length and has 10 segments formed with the eleventh segment nearly complete in its development. The larva illustrated does not contain nurse egg material although it is often found in the gut of larvae of this and later stages. The large ventral vestibule passes food into the long, ciliated esophagus from which it moves to the intestine beginning at segment four. The anus opens in the central portion of the pygidium which has become flattened. The dorsal notch characteristic of the adult pygidium is not present.

The eyes are as in the previous stage, but the palpi are more elongate. Notopodial lobes are present in all the segments. Those of the first segment are located more dorsally than the others and are, thus, nearer the midline. The neuropodial lobes of the first segment are on the same lateral plane as the notopodial lobes of the other segments. This condition prevails in the adult. Branchiae are not present. Melanophores are present on segments three and four as paired dorsal elongations and on the succeeding six segments as paired dots which diminish in size on the more posterior segments. Segments two, seven, and eight have lateral pigment spots. The pygidial melanophore is present. A single stout spine is situated in the notopodium on each side of the modified fifth segment.

Fifteen-Segment Larva, Three Weeks. (Plate III.) This form represents the settling stage of *P. nuchalis.* It is similar in appearance to the adult, but will be discussed here as the final larval stage. It is 0.90 mm. in length and has 15 fully developed segments and a sixteenth partly developed.

The anterior end is adultlike with the peristomium and prostomium greatly developed in comparison with previously described stages. The prostomium is bilobed anteriorly. Two pairs of eyes are located on the prostomium. The nuchal tentacle, one of the diagnostic characters for *P. nuchalis,* is now present on the posterior part of the prostomium. The elongate palpi which arise from the peristomium extend as far as the modified fifth segment. Each of the palpi has a median ciliated groove used in the feeding process. The central body portion, like the anterior portion, resembles that of the adult but the pygidial portion does not. The pygidium is



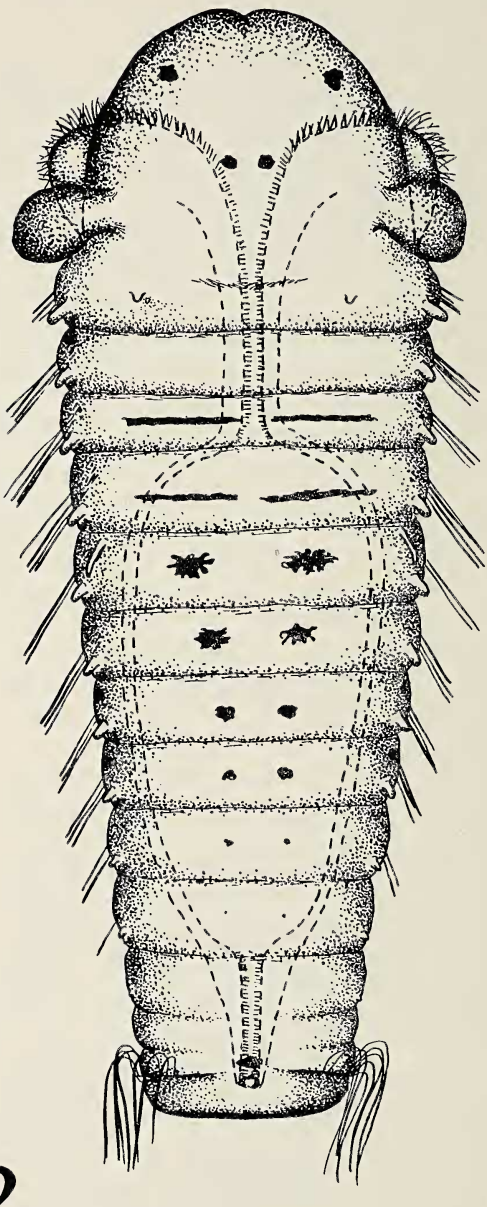


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PLATE II. Fig. 1. 3-setiger larva (six days), 0.30 mm. Fig. 2. 10-setiger larva (two weeks), 0.65 mm.

broad and flangelike but certain changes in ciliary tracts and pigmentation associated with metamorphosis, to be mentioned below, have yet to occur.

The vestibule leads into a long esophagus which joins the intestine at the anterior end of the sixth segment and a long rectum extends from about segment ten to the posterior end of the body. Cilia are present in the vestibule, esophagus, and rectum but are not indicated in the figure.

The prototroch and telotroch are ordinarily lost shortly after settling occurs as one of the changes in the metamorphosis from larva to adult. Gastrotrochs, not mentioned previously, are found on segments three, five, seven, ten, thirteen, and fifteen. These ventral, ciliary tracts first appear on segment three in early stages of development and on succeeding segments (of the numbers mentioned above) as development continues. They are important locomotor organs in the short free-swimming period of *P. nuchalis* and the longer free-swimming periods of forms which hatch at the 3-segment stage.

The conspicuous dorsal melanophores are present only on segments twelve and thirteen and will be lost from these in succeeding stages. The pygidial melanophore and lateral pigment spots present on segment eight and the right side of segment nine are lost in metamorphosis. While in the egg capsule and until shortly after hatching, the larvae are positively phototropic; but at the time of settling and metamorphosis the melanophores and pigment spots are lost and the larvae become negatively phototropic. This suggests rather strongly a functional relationship between the phototropic change and loss of pigmentation.

Two heavy spines are present in each notopodium of the modified fifth segment, the largest of the body segments. Neuropodial hooded hooks appear first in segment seven. Branchiae also appear first on segment seven and in the 15-segment stage are partly formed on segment eight, as well.

The larvae ordinarily hatch at the 12-segment stage, but they may leave the egg case at the 9-segment stage. The larvae settle, metamor-

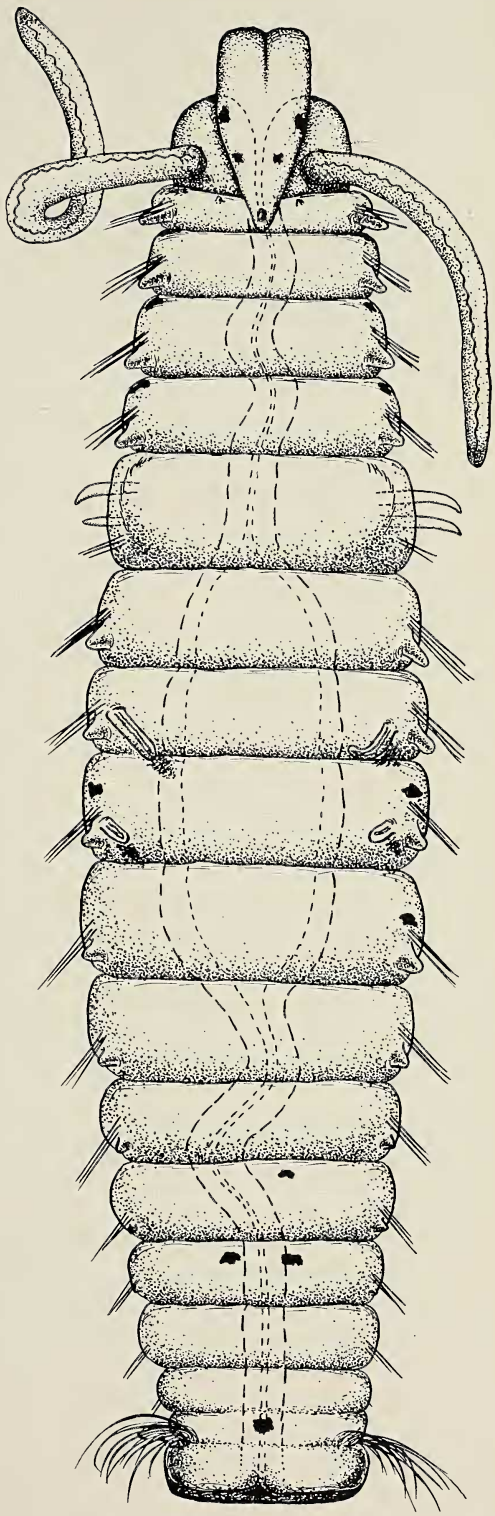

PLATE III. 15-setiger larva (three weeks), 0.90 mm.

phose, and build tubes during the 13- to 17-segment stage.

The adult characteristics are considered in Woodwick (1953).

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